


RESEARCH ARTICLE

Relational structure of illegal wildlife hunting in China: A nationwide hunter–prey network analysis

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Abstract

1. Illegal wildlife hunting continues to pose a major biodiversity threat in China, yet there remains no systemic relational understanding of the way in which perpetrators are linked to key taxa. To address this, here we provide a novel framework for understanding and addressing the systemic roots of wildlife crime.
2. To characterise the structure of hunter–prey interactions in China, we applied bipartite network analysis, a relational framework not previously applied to nationwide wildlife crime prosecution data, to 6379 poaching case prosecution records (2014–2020).
3. Results revealed that illegal hunting forms significantly nested, non-random networks at national and provincial scales, producing a structured socio-ecological system. Offenders were overwhelmingly males, with those aged 31–50 with primary to junior middle school education predominating and hunting the broadest prey spectrum. Provincial socio-economic context, particularly regional wealth, shaped these hunter-prey networks, increasing nestedness in mammal poaching. Key prey families (e.g. Phasianidae) were associated with a broad range of hunter groups (defined by age and educational attainment) within the network.
4. Our findings show that poaching forms a structured, non-random network, suggesting limitations to uniform enforcement approaches in China. This nested structure is consistent with a clear core–periphery configuration, in which a small number of prey families are targeted by many hunter groups, while other prey families are embedded within narrower, more specialised hunting relations. More broadly, effective conservation must integrate demographically targeted interventions, network-informed protection of core prey and regionally tailored policies to disrupt the structure of hunter-prey networks.

KEYWORDS

China, illegal hunting, nestedness, network analysis, poaching, socio-ecological system, wildlife conservation

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1 | INTRODUCTION

Illegal wildlife hunting, commonly termed poaching, represents a critical and persistent driver of global biodiversity loss, contributing directly to population declines, range contractions and the increased extinction risk of numerous terrestrial vertebrates (Benítez-López et al., 2017; Liang et al., 2023; Ripple et al., 2016). Beyond immediate demographic impacts on wildlife, unsustainable hunting disrupts trophic cascades, compromises ecosystem functionality and undermines the conservation efficacy of protected areas, leading to the emergence of 'empty forests' and defaunated landscapes (Dirzo et al., 2014; Harrison et al., 2016). As a multifaceted threat intersecting conservation practice, law enforcement and rural livelihoods, poaching is increasingly recognised not merely as an ecological issue but as a complex socio-ecological phenomenon embedded within specific human contexts (Duffy et al., 2016; Roe et al., 2015). Existing studies have primarily treated poaching as a set of independent events or have focused on main effects of hunter characteristics and socio-economic variables. As a result, the relational structure linking different types of hunters to shared prey assemblages remains poorly understood.

Despite growing academic and policy attention, prevailing approaches to understanding and mitigating poaching often suffer from significant conceptual and methodological limitations (Fukushima et al., 2021). Substantial bodies of research have focused on discrete elements, such as profiling typical offenders, identifying high-value wildlife commodities or correlating poaching incidence with broad socio-economic indicators like poverty (Gavin et al., 2010; Kahler & Gore, 2012; Zhao et al., 2023). While informative, such studies frequently treat poaching events as independent incidents, thereby overlooking the potential for structured, systemic interactions between different hunter group categories and their principal prey assemblages. Consequently, there remains a critical knowledge gap concerning whether illegal hunting operates as a coherent system—characterised by non-random, stable interaction patterns—and how the architecture of such a system might confer resilience against conventional, compartmentalised law enforcement strategies (Narreddy & Shashidhar, 2024; Pires & Moreto, 2011). This gap highlights the need for analytical frameworks that can capture the relational complexity of poaching (Fukushima et al., 2021; Roe et al., 2015).

Network theory, widely applied in ecology to study mutualistic and antagonistic species interactions, provides a powerful paradigm with which to address this limitation (Bascompte et al., 2003; Delmas et al., 2019; Huang, Newman, et al., 2021). Using a bipartite network approach, the connections between two distinct sets of nodes, here, hunters and prey, can be modelled (Dormann et al., 2009). Key topological properties, such as nestedness—a pattern where specialists interact with subsets of the partners of generalists—can reveal core species and perpetrator profiles that stabilise the entire system (Almeida-Neto et al., 2008; Memmott et al., 2004). From a relational perspective, nestedness captures a core–periphery structure in which a small set of prey taxa function as shared relational hubs, linking otherwise distinct hunter group categories (Bascompte

et al., 2003). Identifying such relational cores is important because interventions that disrupt these shared relations may generate system-wide effects that cannot be achieved by targeting individual actors alone (Pires & Moreto, 2011). Applying this framework to illegal hunting allows for a shift in focus from individual infractions to an analysis of system-level architecture, potentially identifying leverage points for more effective and targeted interventions that disrupt the network's core rather than its periphery (Pires & Moreto, 2011).

Within such systems, prey species are not equally targeted; rather, hunting pressure varies among species, driven by differences in biological traits, legal status and market demand. Across taxa, hunters tend to target species that offer higher returns relative to effort and risk, including larger-bodied species, those with greater economic or cultural value and those subject to weaker protection or enforcement (Benítez-López et al., 2017; Ni et al., 2022; Ripple et al., 2016). Recent work further demonstrates that prey traits such as body mass, rarity and protection status systematically shape exploitation patterns and can determine which taxa emerge as disproportionately targeted cores within wildlife exploitation systems (Fukushima et al., 2021; Liang et al., 2023; Zhao et al., 2023). In a network context, such trait-mediated selectivity is expected to structure interaction patterns, with heavily targeted prey forming shared targets across multiple hunter group categories and contributing disproportionately to network cohesion and persistence.

China presents a critical and instructive context for such an investigation. Despite governance through a stringent legal framework, illegal hunting remains a significant conservation challenge (Huang, Ping, et al., 2021; Shao et al., 2021; Xiao et al., 2021; Zhao et al., 2023; Zhou et al., 2020). The systematic availability of judicial records through the China Judgements Online platform has enabled unprecedented access to nationwide prosecution data, providing a novel empirical basis for large-scale analysis (Liang et al., 2023; Xiao & Ye, 2025). While recent studies have begun to utilise these data to explore spatial and temporal trends in wildlife crime (Ye et al., 2020; Zhao et al., 2023), a comprehensive examination of the structured interactions between hunter demographics and prey taxa, analysed through a formal network lens, remains conspicuously absent. Given China's vast socio-economic gradients, diverse biomes and central role in regional wildlife trade dynamics (Huang, Newman, et al., 2021), a nationwide network analysis examining poaching is both feasible and urgently needed to inform context-specific policy and enforcement.

While previous studies have examined correlations between poaching and individual-level demographics (Shao et al., 2021) or provincial socio-economic conditions (Zhao et al., 2023), these studies have typically treated poaching incidents as independent events and have not examined the structure of interactions linking hunter groups to shared prey assemblages. To our knowledge, no study has applied bipartite network analysis to model these relationships using nationwide prosecution data. We address this gap by adopting a network perspective.

This study makes three contributions. First, we apply nestedness analysis to characterise poaching as a structured set of interactions

between hunter groups and prey families, rather than as isolated events. Second, we test how hunter age and education interact with provincial socio-economic conditions to shape prey spectrum width, moving beyond main-effect analyses to examine conditional relationships. Third, we identify prey families that contribute disproportionately to network structure and test whether body mass, IUCN status and protection status predict targeting intensity, linking network organisation to prey traits. Collectively, these analyses shift the focus from identifying who poaches and what is poached to understanding how hunting interactions are organised across groups and taxa, providing a structural perspective with potential implications for targeted conservation interventions.

Building on this framework, we construct bipartite networks to examine how illegal hunting in China is organised as a series of interactions between hunter socio-demographic groups and prey families. Because prosecution records provide cross-sectional observations rather than longitudinal behavioural histories, we focus on age-structured positions within these networks rather than inferring temporal change. We therefore interpret age as a positional indicator of experience, skill and livelihood context within the network, not as evidence of cohort effects or behavioural trajectories. We address two research questions, grounded in ecological and socio-economic theory:

1. Do hunter–prey interactions form non-random, nested networks at national and provincial scales?
2. How are these network structures associated with the interaction between hunter socio-demographics (age and education) and provincial socio-economic conditions?

These questions lead to three testable hypotheses:

H1. Hunter–prey networks will exhibit significant nestedness, consistent with ecological network theory predicting that generalist actors interact with widely shared resources, while more specialised actors interact with subsets of these (Almeida-Neto et al., 2008; Bascompte et al., 2003; Mariani et al., 2019).

H2. Middle-aged individuals with intermediate education levels will occupy more central positions within the network, consistent with human capital and routine activity theory, which suggest that this group may combine practical capability with constrained livelihood alternatives (Cohen & Felson, 1979; Oreopoulos & Salvanes, 2011; Schultz, 1961).

H3. Provincial socio-economic conditions, particularly regional wealth, will be associated with variation in network structure and prey targeting patterns, consistent with theories of development and market transition that link economic context to resource use and exploitation (Cao, 2020; Liu et al., 2007).

Together, these analyses aim to characterise how hunting interactions are structured across hunter groups and prey taxa, and to identify which components of this structure may be most relevant for targeted intervention. By combining network analysis with demographic and socio-economic data, this study provides a structural perspective on illegal hunting that complements existing individual- and species-level approaches.

2 | METHODS

2.1 | Sourcing and defining data on poaching offences

A ‘poacher’ was defined as any perpetrator conducting any domestic hunting practice without an authorisation permit under China's Wild Animal Protection Law (1988, 2016, 2022); by contrast, trans-border offences would be prosecuted separately as smuggling/trafficking, which we do not examine here. In China, all wildlife resources are the property of the state and any hunting of species on China's List of Fauna under Special State Protection (1988, 2021) or List of Species with Important Ecological, Scientific, or Social Value (2000, 2023) is liable to prosecution under the Wild Animal Protection Law. An offence includes any illicit taking, transport or trade of animals, animal parts and derivatives thereof. In addition, in February 2020, the Standing Committee of the National People's Congress implemented a permanent ban on trading terrestrial wild (non-livestock) animals for consumption as food (Xiao et al., 2021), including un-listed ‘vermin’ species, as amended to the Wild Animal Protection Law (2022; Article 24). Furthermore, the ownership of any firearm or wild animal trap by a private citizen is forbidden under China's Criminal Law (1997), although Article 24 of the Wild Animal Protection Law does permit authorised personnel with gun licences issued by the Public Security Authority to hunt for the purpose of animal control and management. The combination of these laws and prohibitions precludes any opportunity for hunting to be conducted as a field sport or legitimate recreational activity in China. Instead, illegal hunters that kill protected animals for food, as a tradable commodity, or to protect property/ crops, do so mindful that this places them in jeopardy of prosecution, where anyone convicted of illegal hunting in China could face up to 15 years fixed-term imprisonment accompanied by fines and/or the confiscation of property (Shao et al., 2021; Zhou et al., 2016).

Documents containing the terms ‘wild animal’ (野生动物), ‘illegal hunting’ (非法狩猎) and ‘illegal catching’ (非法猎捕) were obtained from the China Judgements Online website (<https://wenshu.court.gov.cn/>), archived between 1 January 2014 and 31 December 2020. This website was established in accord with the Provisions of the Supreme People's Court on the Publication of Judgement Documents by People's Courts on the Internet (2014) to systematically make available all anonymised judgement documents issued by the People's Courts as a means to publish crime rates across all governmental levels. The OpenLaw database, a nationwide database established by the Open Law Alliance non-governmental organisation,

provides a complementary and independent source of prosecution data. The number of illegal hunting verdicts from Jan 2014 to March 2020 listed on this source was, however, quite similar to the number recorded by the China Judgements Online database (Liang et al., 2023). We therefore sourced data from the China Judgements Online database due to its official status and comprehensive coverage and mandatory prosecution record upload requirements, as used in previous research investigating wildlife crime in China (Shao et al., 2021; Zhao et al., 2023). After reaching a peak of 23.389 million in 2020, the total number of judgement documents (across all crime types) published on the China Judgements Online platform declined by 29% in 2021, 46% in 2022 and 64% in 2023. This reduction results from a system-wide change in public disclosure practices, introduced to prevent improper release of sensitive information and to protect privacy and public interests. As a result, post-2020 records are not consistently available across crime categories. We therefore restrict our analysis to 2014–2020, the period during which data availability for poaching cases was relatively stable and complete.

From the 10,937 poaching offence judgement documents we obtained, we manually reviewed the introduction of the defendant, the prosecutors' allegation, the defendants' statements and the court's factual findings. We excluded those documents that did not: (i) relate to the poaching of either birds or mammals (2667 documents), (ii) include poacher age or educational attainment (1778), (iii) include information referring to prey family (102) or that (iv) involved a retrial judgement (11). The remaining dataset we used in bipartite network analyses comprised 6379 cases, 4149 pertaining to bird poaching and 2428 to mammal poaching, which involved 14,784 perpetrators, 10,036 of whom poached birds and 5095 poached mammals; a further 198 cases involved 347 offenders prosecuted for poaching both birds and mammals, and for these cases, offenders were included in analyses relating to both taxonomic classes.

2.2 | National and provincial hunter–prey network interactions

To examine network interactions between hunter groups and prey, we extracted data on the perpetrator's age and educational attainment from the defendant description and identified prey species from the court's factual findings. Because prosecution records provide cross-sectional observations rather than longitudinal behavioural histories, we treat age as a positional attribute within the network rather than as evidence of cohort effects or temporal change.

We limited our analysis to male hunters, who comprised the vast majority of cases (Edlund et al., 2013), and classified them into 20 socio-demographic groups defined by age (≤ 30 , 31–40, 41–50, 51–60, ≥ 61) and educational attainment (no schooling, primary school, junior middle school and senior middle school or above). This grouping allows comparison of relational positions across socio-demographic categories while maintaining sufficient connectivity for network analysis (Shao et al., 2021).

Prey were classified into 68 bird families (416 species in 19 orders; Table S1) and 25 mammal families (96 species in 10 orders; Table S2). Classification at the family level increases network connectivity by aggregating species into broader taxonomic units, while reducing species-level resolution (Shao et al., 2021).

On this basis, we constructed adjacency matrices (M) to represent bipartite networks linking two sets of nodes: hunter socio-demographic groups (X) and prey families (Y). Each matrix element $m_{ij} = 1$ if hunter group i was associated with prey family j , and otherwise $m_{ij} = 0$. A hunting 'link' was defined as the capture or killing of at least one individual from a given prey family by a member of a hunter group.

To reduce the influence of variation in detection, prosecution and reporting, we analysed the presence or absence of interactions rather than their frequency (Liang et al., 2023). All quantitative interactions were therefore converted to binary form to focus on network topology rather than the number of individuals involved. Because prosecution records were anonymised, it was not possible to identify repeat offenders across cases.

We constructed separate national networks for bird and mammal prey, as well as provincial-level networks (29 bird networks and 27 mammal networks) across mainland China's 31 provincial administrative divisions (Figures S1 and S2).

At the network level, we quantified nestedness using the Network Overlap and Decreasing Fill metric (Almeida-Neto et al., 2008) for each adjacency matrix (Mariani et al., 2019). Nestedness describes the extent to which interactions of less-connected nodes form subsets of those of more-connected nodes, capturing asymmetry in the distribution of links within the network. In this context, a nested network indicates that interactions of less-connected hunter groups form as subsets of those of more-connected groups, or that less-targeted prey families are associated with subsets of the hunter groups exploiting more widely targeted families.

To assess whether observed network structure differed from random expectation, we compared empirical network metrics with those generated from 1000 null model iterations based on binary matrices. Null matrices were generated using the Curveball algorithm, which preserves row and column totals while sampling uniformly from the space of possible matrix configurations (Strona et al., 2014).

To facilitate comparisons among provincial networks, we standardised nestedness as Z-scores (Sebastián-González et al., 2015):

$$Z = \frac{\text{Observed} - \text{Mean}_{\text{null}}}{\text{SD}_{\text{null}}}$$

where Observed is the empirical nestedness of a given network, $\text{Mean}_{\text{null}}$ is the mean nestedness across null matrices and SD_{null} is the corresponding standard deviation.

Of the 29 bird networks constructed, two (Xinjiang and Shanghai) were excluded from further analyses due to insufficient data to calculate standardised nestedness. All network analyses and visualisations were conducted in R using the package *bipartite* (Dormann et al., 2024).

Across provinces, we compiled nine socio-economic variables from regional statistical yearbooks and bulletins (2017–2020), obtained from the China Knowledge Resource Integrated Database (<http://www.cnki.net/>) and government websites. Because individual-level socio-economic status was not available, these variables were used to characterise the broader regional context in which offences occurred. The variables selected have previously been associated with variation in poaching patterns in China (Zhao et al., 2023).

Provincial-level values ($N=31$) were applied to all prefectures within each province ($N=337$). To address multicollinearity among variables, we performed a varimax-rotated principal component analysis (PCA). Three principal components were retained: (i) *regional wealth*, with high loadings for resident population size (0.99), GDP (0.91), rural population size (0.87) and total retail sales of consumer goods (0.92); (ii) *per capita income*, with high loadings for per capita GDP (0.90) and disposable income of urban (0.92) and rural households (0.90); and (iii) *educational attainment level*, with high loadings for mean years of education beyond age 15 (0.91) and the proportion of the population with at least junior secondary education (0.74). Together, these components explained 95% of the total variance (Table S3).

To characterise variation in prey use across the network, we quantified the contribution of each prey family to overall nestedness using Z-scored nestedness values relative to null models (Dormann et al., 2024). This approach accounts for differences in node degree (i.e. the number of connections a node has within the network) and enables comparison of relative contributions across prey families. 'Targeting intensity' is defined here as the frequency with which a prey family is linked to hunter groups, operationalised as its nestedness contribution. This metric captures observed associations within the network rather than underlying preference or motivation. A positive nestedness contribution indicates that a prey family is associated with a broad range of hunter groups, whereas a negative value indicates more restricted associations (Saavedra et al., 2011). The prey spectrum width of each hunter group was defined as the proportion of prey families it was associated with relative to the total number of prey families in the network.

We compiled prey trait data for *body mass*, *IUCN risk category* and *protection status*. Body mass was obtained from published sources (Etard et al., 2020) and China's national database (<http://museum.ioz.ac.cn/>). IUCN risk categories were obtained from the IUCN Red List (<https://www.iucnredlist.org/>) and coded ordinally from least to most threatened. Protection status was based on China's List of Fauna under Special State Protection (1989), coded according to level of protection. To reduce differences in scale among variables, body mass was log-transformed prior to analysis. Because phylogenetic generalised least squares models require continuous predictors, IUCN risk category and protection status were treated as ordinal variables (Yin et al., 2020). For each prey family, mean values of body mass, IUCN risk category and protection status were

calculated from constituent species. For phylogenetic analyses, one representative species was selected per family. Phylogenetic trees for birds and mammals were obtained from VertLife (<http://vertlife.org/>), using the datasets of Jetz et al. (2012) and Upham et al. (2019), respectively (Figures S3 and S4).

We used ordinary least squares models to test whether provincial-level socio-economic and environmental factors were associated with (1) the standardised nestedness of provincial networks, (2) the prey spectrum width of hunter groups and (3) the nestedness contribution of prey families (see Table S4 for corresponding hypotheses). Provincial polygons were obtained from the Resource and Environment Science and Data Center (Chinese Academy of Sciences; <http://www.resdc.cn>). To assess spatial autocorrelation in model residuals, we conducted Moran's I, Lagrange multiplier and robust Lagrange multiplier tests using rook contiguity-based spatial weights (Weisburd et al., 2022). Where spatial dependence was detected, spatial lag and/or spatial error models were fitted using maximum likelihood estimation. All ordinary least squares models, spatial diagnostic tests and spatial regression analyses were conducted in GeoDa 1.22 (Anselin & Rey, 2014).

We assessed the effects of hunter socio-demographic factors on prey spectrum width and the effects of taxonomic grouping (family or order) on nestedness contribution across provinces. Shapiro–Wilk tests indicated that the assumptions of normality were not met for either response variable. We therefore used the nonparametric Scheirer–Ray–Hare test to evaluate the effects of age and educational attainment on the proportion of prey families targeted by each hunter group within provinces. Kruskal–Wallis tests, followed by Dunn's post hoc comparisons, were used to identify pairwise differences among age and education classes, as well as differences in nestedness contribution among prey taxa for both birds and mammals. All analyses were conducted in R using the package FSA (Ogle et al., 2023).

To analyse variation in nestedness contribution, we fitted phylogenetic generalised least squares models with an explicit covariance structure. Nestedness contribution was modelled as a function of *body mass*, *IUCN risk category* and *protection status* (see Table S5 for corresponding hypotheses), using the *pgls* function in the R package caper (Orme et al., 2023). The phylogenetic scaling parameter (λ) was estimated for each model, ranging from 0 (phylogenetic independence) to 1 (complete phylogenetic dependence) (Freckleton et al., 2002).

In this study, 'relations' refer to bipartite associations between hunter socio-demographic groups and prey families, defined by co-occurrence in prosecution records. A relation exists if at least one offender from a given age-by-education group was prosecuted for hunting at least one species from a given prey family. These relations do not represent direct social interactions among hunters (e.g. co-offending, communication or trade), and our analysis is therefore structural rather than interactional.

Significance was set at $p < 0.05$ for all analyses.

3 | RESULTS

3.1 | Network-level nestedness of hunter-prey interactions

To test H1, we first assessed whether hunter-prey networks exhibited nested structure. At the national level, both bird and mammal networks were more nested than expected under null models (Table S6). Figure 1 illustrates the resulting pattern, in which a subset of prey families (e.g. Phasianidae) and hunter groups are associated with a large proportion of interactions and hunter groups (e.g. age 41–50, primary school) occupy central positions, while others are linked to subsets of these associations.

At the provincial level, networks were also more nested than expected by chance for both bird ($n=27$; Figure S1) and mammal ($n=27$; Figure S2) poaching (Table S7). Spatial regression analyses indicated no association between provincial socio-economic variables and nestedness in bird networks. By contrast, nestedness in mammal networks was positively associated with regional wealth (Table S8).

3.2 | Hunter demographics shape prey spectrum width

To test H2, we examined how hunter socio-demographic characteristics were associated with prey spectrum width across provincial networks. Age and educational attainment both had significant effects on the proportion of available prey families targeted by each hunter group

(Figure 2; Table S9). For both bird and mammal networks, hunters aged 41–50 poached significantly more families than those aged ≤ 30 and ≥ 61 (Table S10). Similarly, for both bird and mammal networks, primary school and junior middle school educated groups poached significantly more families than those with no schooling and those with senior middle school or above (Table S11). These patterns varied across provincial socio-economic contexts, with regression analyses indicating

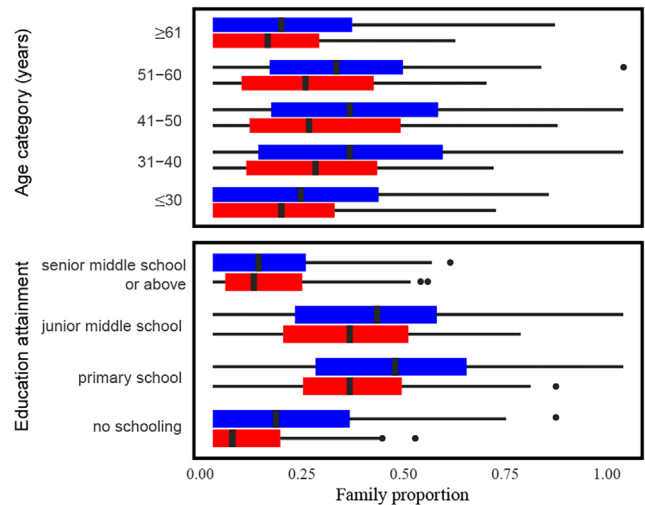


FIGURE 2 Box and whisker plots of the proportion of provincial bird (red) and mammal (blue) family poaching contributed by each hunter group in relation to hunter age and education class. Box plots show the median (horizontal line), first and third quartiles (box), and the range of values excluding outliers (whiskers).

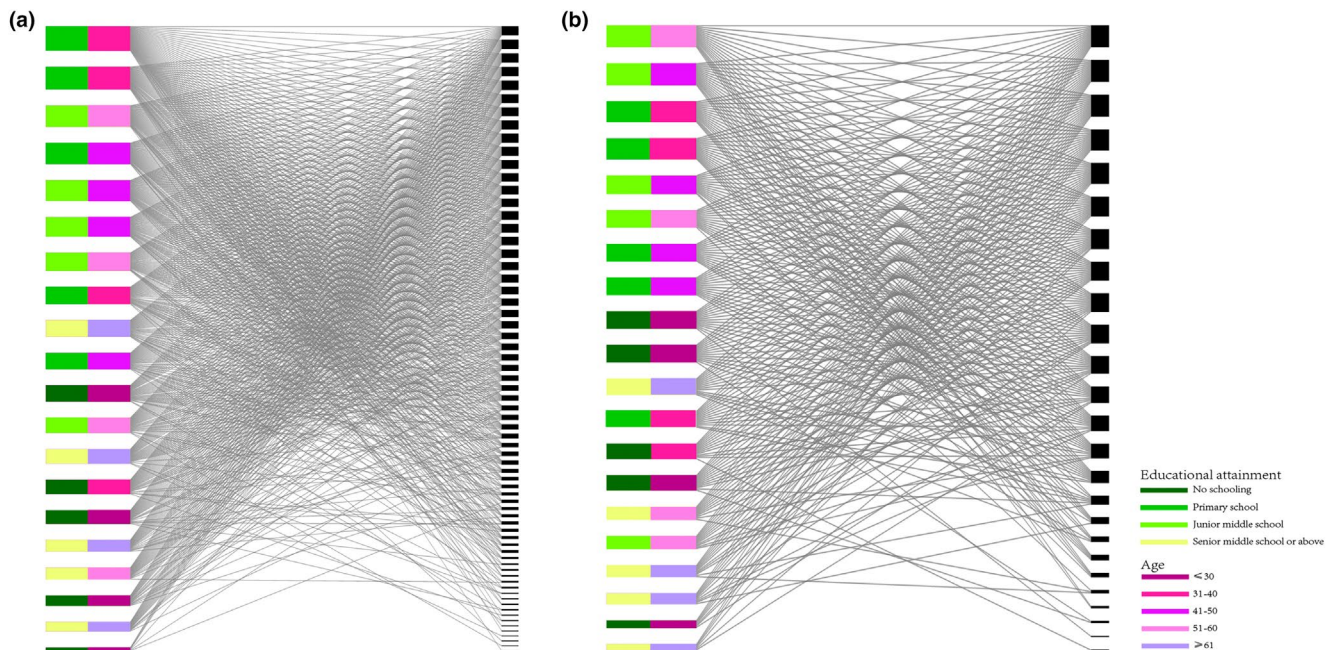


FIGURE 1 Bipartite interaction networks depicting hunter group links with bird (a) and mammal (b) families poached across China. Hunter groups are colour-coded to indicate age and educational attainment classes on the left of each figure panel, with those prey families poached on the right. Relationships are scaled in descending order according to the total number of binary links associated with each node. Node size reflects the number of relational links, highlighting core-periphery structure.

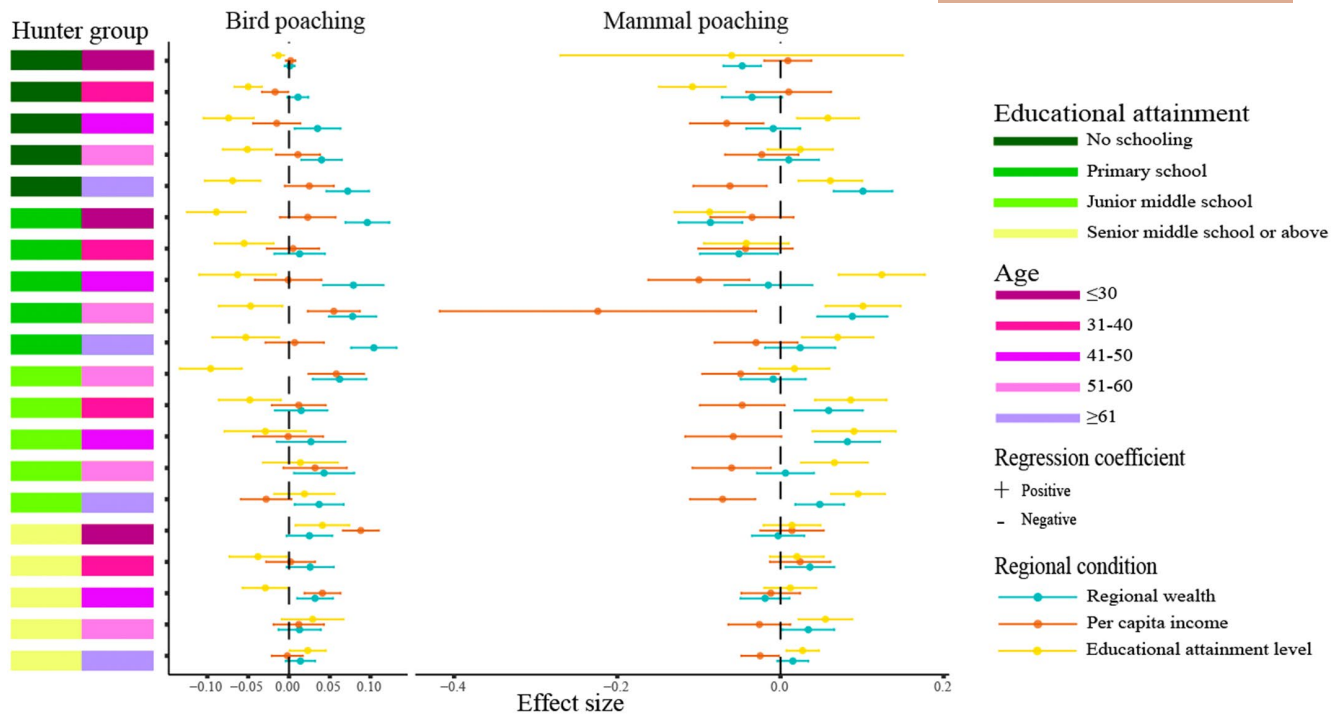


FIGURE 3 Hunters' prey spectrum widths for bird and mammal poaching with either positive or negative coefficient values in regression models with regional wealth, per capita income or educational attainment level. Horizontal bars indicate 95% confidence intervals that do not overlap zero.

associations between regional conditions and prey spectrum width (Figure 3; Tables S12 and S13).

3.3 | Prey targeting intensity and its correlates

To test H3, we examined how prey targeting intensity (nestedness contribution) varied with taxonomic grouping, prey traits and provincial socio-economic conditions. Across provinces, targeting intensity differed among bird families, with Phasianidae consistently showing higher values than Falconidae, Phylloscopidae, Strigidae and Zosteropidae (Figure S5). By contrast, no significant differences in targeting intensity were detected among mammal families (Figure S6). In national networks, targeting intensity in birds was positively associated with body mass (Figure S7; Table S14), while in mammals, it was associated with protection status, with less-protected families showing higher values (Figure S8; Table S15). These associations varied across provinces. Additional analyses indicated that relationships between targeting intensity and prey traits were associated with variation in provincial socio-economic conditions (Figures S9 and S10; Tables S16 and S17).

4 | DISCUSSION

Consistent with H1, hunter-prey networks were significantly nested at both national and provincial scales, indicating a structured pattern of interactions linking hunter groups to shared prey taxa. In these networks,

a subset of prey families (e.g. Phasianidae) was associated with a broad range of hunter groups, while other families were linked to subsets of these interactions. Such patterns are characteristic of nested ecological networks, in which more specialised actors interact with subsets of the partners of more generalised actors (Bascompte et al., 2003). Interpreted in this context, the observed nestedness is consistent with a core-periphery structure in which some prey families are more widely targeted across hunter groups. This overlap may contribute to the persistence of hunting pressure, as interactions are not confined to isolated hunter-prey pairs, although our cross-sectional data do not allow direct inference about temporal dynamics. More broadly, these findings suggest that hunting activity is structured around shared associations between hunter groups and commonly targeted prey families, rather than independent or isolated interactions. From a management perspective, this structure implies that interventions focusing on widely targeted prey families may affect a broader range of hunter groups than approaches targeting individual offenders or less-connected species (Memmott et al., 2004; Pires & Moreto, 2011).

Consistent with H2, offender demographic patterns were highly structured, with hunters predominantly male, concentrated in the 31-50 age classes and most commonly having primary to junior middle school education. These groups also exhibited broader prey spectra, targeting a larger proportion of available prey families within provincial networks. This pattern is consistent with expectations from human capital and routine activity theory, which suggest that middle-aged individuals with intermediate education may combine practical capability with more limited access to alternative livelihoods (Cohen & Felson, 1979).

Age-related variation in prey spectrum width provides further context for H2. Middle-aged individuals, particularly those aged 41–50, were associated with the broadest prey spectra across both bird and mammal networks, whereas younger (≤ 30) and older (≥ 61) groups were linked to narrower ranges. This pattern aligns with the expectation that hunting activity is shaped by a combination of experience, physical capacity and socio-economic role, as suggested by studies of resource extraction and criminological life-stage theory (Gurven et al., 2006; Hill & Kintigh, 2009; Sampson & Laub, 1995; Steffensmeier et al., 2025). However, our data do not directly measure hunting skill or knowledge, and alternative explanations, such as differences in time availability, economic pressure or access to equipment, cannot be excluded. The broader prey spectra observed in middle-aged groups may also be associated with their role as primary household providers, leading to more generalised resource-use strategies (Brashares et al., 2004). By contrast, narrower prey spectra among younger individuals may be associated with more limited experience or differing livelihood strategies (Liang et al., 2023; Shao et al., 2021). Similar age-structured patterns in hunting and resource use have been reported in other socio-ecological systems (Ingram et al., 2025; Knoop et al., 2020), suggesting that these dynamics are not unique to the Chinese context.

Educational attainment also showed a non-linear association with prey spectrum width, providing further context for H2. Hunter groups with primary and junior middle school education targeted a broader range of prey families than those with no schooling or higher levels of education. This pattern supports the possibility that intermediate levels of education are associated with increased capacity for resource use without necessarily providing access to alternative livelihoods, as suggested by human capital theory (Oreopoulos & Salvanes, 2011; Schultz, 1961). However, our data do not directly measure skill, income or employment status, and other explanations—such as the distribution of education levels within rural populations—cannot be excluded. Lower prey spectrum width among individuals with no formal schooling may be associated with more limited access to resources or lower operational efficiency, whereas narrower spectra among more highly educated individuals may relate to alternative livelihood opportunities or differing risk preferences (Kideghesho et al., 2007; Kollmuss & Agyeman, 2002). These patterns highlight the importance of considering how education interacts with livelihood context in shaping hunting behaviour.

Consistent with H3, targeting intensity varied across prey taxa, with certain bird families, particularly Phasianidae, showing consistently higher values across networks. This pattern aligns with ecological theory suggesting that resource use reflects trade-offs between energetic return and acquisition cost (Nonacs, 2001; Stephens & Krebs, 1986). Larger-bodied, ground-dwelling or more detectable species may therefore be more frequently represented in hunter–prey associations (Benítez-López et al., 2017; Shao et al., 2021). However, we interpret high targeting intensity as an empirical pattern rather than evidence of preference. Alternative explanations include differences in local abundance, detectability, legal protection and market demand. Our data do not allow these

mechanisms to be distinguished, and further work incorporating independent measures of prey availability and hunter behaviour would be required. More broadly, these results indicate that variation in targeting intensity is associated with the combined influence of prey traits and broader socio-economic context, rather than a single underlying driver.

Further evidence supporting H3 comes from variation in the relationship between socio-economic conditions and network structure across provinces. Greater regional wealth was associated with higher nestedness in mammal poaching networks, but not in bird networks, indicating that socio-economic context influences patterns of hunter–prey interactions in a taxon-specific manner. This finding aligns with broader theories linking economic development to shifts in resource use and market integration (Liu et al., 2007; Zayonc et al., 2025). However, our data do not allow direct inference about the underlying mechanisms, and differences between bird and mammal networks may reflect variation in prey ecology, market structure or cultural practices. More generally, these findings highlight that the relationship between socio-economic conditions and illegal hunting is context-dependent (Brashares et al., 2011; Commerçon et al., 2021; Zhou et al., 2014, 2015), suggesting that patterns observed at the national level may mask important regional variation (Ni et al., 2022; Redpath et al., 2015; Ye et al., 2020).

In general, this study adds a relational and structural perspective that complements prior analyses. Specifically, where previous work has shown that middle-aged men with intermediate education are most frequently involved in poaching, our results indicate that these groups also occupy more central positions within hunter–prey networks. Where earlier studies identified that certain species are more frequently targeted, our analysis shows that these species (e.g. Phasianidae) are associated with a broader range of hunter groups within the network. Finally, where prior work examined main effects of socio-economic variables, our results indicate that regional conditions are associated with variation in who targets which prey, highlighting relationships not captured by additive models. We do not claim to identify entirely new empirical patterns; rather, we provide a structural perspective on existing data that reveals how hunting interactions are organised across hunter groups and prey taxa, with implications for understanding potential intervention strategies.

A key limitation concerns the interpretation of relational structure. Our bipartite networks capture associations between hunter socio-demographic groups and prey families based on co-occurrence in prosecution records, and do not represent direct social interactions among offenders (e.g. co-offending, communication or trade relationships). Accordingly, references to ‘hubs’ or ‘overlapping relations’ describe structural patterns in these data rather than evidence of social coordination. Inferring social organisation from these associations would be inappropriate, and future work incorporating co-offending data or social network analysis would be required to address this question. A second limitation relates to the temporal scope of the data. Our findings apply most directly to the 2014–2020 period, and we cannot assess whether the same structural patterns persist in more recent years. While some aspects of these

patterns may relate to relatively stable socio-ecological conditions, this cannot be assumed. Our aim is therefore to characterise the organisation of hunter–prey interactions during a period of relatively complete data, rather than to infer temporal trends. Future research should re-examine these relationships as more recent data become available.

5 | CONCLUSIONS

As with all studies based on prosecution records, the networks we describe represent detected and adjudicated offences rather than the full extent of illegal hunting activity, and should therefore be interpreted as representations of enforcement–visible interactions rather than absolute prevalence (Gavin et al., 2010). Within this scope, our findings highlight the value of a structural perspective on illegal hunting. By identifying widely shared prey–hunter associations within nested networks, the analysis points to potential leverage points where reducing access to or targeting of key prey families may affect a broad range of hunter groups simultaneously, complementing approaches focused on individual offenders (Pires & Moreto, 2011). More broadly, the results suggest that illegal hunting can be understood not only as a series of discrete events, but also as a structured outcome of interacting demographic, educational, socio-economic and ecological factors (Duffy et al., 2016; Fukushima et al., 2021; IPBES, 2019; Ostrom, 2009; Roe et al., 2015). This perspective highlights limitations of uniform, one-size-fits-all enforcement strategies and supports the development of more targeted and context-specific interventions (Wellsmith, 2011). In practice, this may involve combining: (i) interventions that address the demographic hunter groups most strongly represented in the network, including the provision of alternative livelihood pathways; (ii) enforcement strategies that prioritise widely targeted prey families; and (iii) geographically tailored policies that account for variation in regional socio-economic conditions (Brooks et al., 2012; Liu et al., 2007; Ni et al., 2022).

Together, these findings illustrate how integrating network analysis with socio-ecological data can contribute to a more nuanced understanding of wildlife exploitation and support the development of conservation strategies that are better aligned with the structure of the systems they aim to manage. This integrated perspective bridges conservation science, criminology and development economics, and highlights the need for policies that match the complexity and adaptability of the socio-ecological systems they aim to manage (Fukushima et al., 2021; Ostrom, 2009; Petrosillo et al., 2009).

AUTHOR CONTRIBUTIONS

Yi Luo, Xiao Xiao and Zhao-Min Zhou conceived the concept. Mei-Ling Shao, Yi-Xiao Li and Yuan-Yuan Cao performed data collection and extraction. Yi Luo, Xiao Xiao and Zhao-Min Zhou analysed these data. Chris Newman and Zhao-Min Zhou led the writing of the manuscript. All authors contributed critically to drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare no competing interests.

DATA AVAILABILITY STATEMENT

The court verdicts are available in the China Judgements Online website (<https://wenshu.court.gov.cn/>). Provincial polygons are available in the Resource and Environment Science and Data Center (Chinese Academy of Sciences; <http://www.resdc.cn>). R code for network analysis, adjacency matrices to represent bipartite networks linking hunter socio-demographic groups and prey species, socio-economic variables at provincial level and species traits for birds and mammals were uploaded to Mendeley Data, <https://data.mendeley.com/datasets/dt87fyc424/1>.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Figure S1. Bipartite interaction networks for bird poaching across 29 provinces. Each panel represents one province; left nodes are hunter groups (age × education); right nodes are prey families. The nested

structure visible in most provinces supports the main text's claim that nestedness is a general property across regions.

Figure S2. Bipartite interaction networks for mammal poaching across 27 provinces. Each panel represents one province; left nodes are hunter groups (age × education); right nodes are prey families. The nested structure visible in most provinces supports the main text's claim that nestedness is a general property across regions.

Figure S3. A phylogeny of bird species representing those families (in parentheses) included in our analysis, generated from VertLife (<http://vertlife.org>).

Figure S4. A phylogeny of mammal species representing those families (in parentheses) included in our analysis, generated from VertLife (<http://vertlife.org>).

Figure S5. Box and whisker plots of nestedness contribution in relation to bird family. Box plots show the median (horizontal line), first and third quartiles (box) and range of values excluding outliers (whiskers). Differences were significant (Kruskal–Wallis chi-squared = 106.866, $p < 0.001$). Dunn's Kruskal–Wallis multiple comparisons showed that nestedness contributions were significantly greater in Phasianidae (highlighted in red) than that in four families (in green; Falconidae (Bonferroni adjusted $p = 0.036$), Phylloscopidae (0.021), Strigidae (0.026) and Zosteropidae (< 0.001)).

Figure S6. Box and whisker plots of nestedness contribution in relation to mammal family. Differences were insignificant among families (Kruskal–Wallis chi-squared = 23.443, $p = 0.490$).

Figure S7. Effect sizes on prey nestedness contribution for bird poaching in relation to *protection status* as given by the List of Fauna under Special State Protection (1988) and the *IUCN risk category*, as well as *body mass*.

Figure S8. Effect sizes on prey's nestedness contribution for mammal poaching in relation to *protection status* as given by the List of Fauna under Special State Protection (1988) and the *IUCN risk category*, as well as *body mass*.

Figure S9. Effect sizes of *regional wealth*, *per capita income* and *educational attainment level* on the nestedness contribution of bird families.

Figure S10. Effect sizes of *regional wealth*, *per capita income* and *educational attainment level* on the nestedness contribution of mammal families.

Table S1. Summary of bird species poached by 20 hunter socio-demographic groups (constructed in relation to hunter age and educational attainment) in China, along with the number of provinces in which these bird species were poached. Protection status relates to the List of Fauna under Special State Protection (1988), threatened status relates to that designed by the IUCN Red List of Threatened Species and body mass was obtained from the trait data compiled by Etard et al.¹

Table S2. Summary of mammal species poached by 20 hunter socio-demographic groups (constructed in relation to hunter age and educational attainment) in China, along with the number of provinces in which these bird species were poached. Protection status relates to the List of Fauna under Special State Protection

(1988), threatened status relates to that designed by the IUCN Red List of Threatened Species and body mass was obtained from the trait data compiled by Etard et al.¹

Table S3. Factor loadings for nine variables and three regional factors across 31 provincial administrative regions in mainland China. Heavy loadings of variables on regional factors are given in bold.

Table S4. Predicted responses of network standardised nestedness, poaching spectrum width of hunter groups and nestedness contribution of prey taxonomic families to provincial socio-economic environmental factors.

Table S5. Hypothesised responses of nestedness contribution of prey families to the taxonomic family traits.

Table S6. Topological structure properties (connectance, nestedness, modularity, robustness) for the national bird and mammal networks. Numbers in parentheses for nestedness refer to 95% confidence intervals generated from 1000 randomization procedures; + indicates that the observed value is significantly higher than the index values from the randomised data set; - indicates that the observed value is significantly lower than the index value from the randomised data set.

Table S7. Summary of the topological features of the hunter-prey networks for each provincial network, including standardised nestedness and 95% confidence intervals from null models. All observed nestedness values are significantly higher than null expectations. Numbers in parentheses refer to 95% confidence intervals generated from 1000 randomization procedures; + indicates that the observed value is significantly higher than the index value from the randomised data set; - indicates the observed value is significantly lower than the index value from the randomised data set; NA indicates that value is not available due to data structure.

Table S8. Results of univariate regression analyses (Ordinary Least Squares) for the standardised nestedness of provincial networks in relation to each regional factor. Spatial autocorrelation was not detected using Moran's I. Bold highlights indicate when the model effectively explained nestedness.

Table S9. Scheirer-Ray-Hare test results showing significant main effects of age and education, as well as their interaction, on the proportion of bird and mammal families poached per province.

Table S10. Results of Dunn's Kruskal-Wallis multiple comparisons identifying which age group differ significantly from each other, in relation to the proportion for bird (red) and mammal (blue) families poached. *p*-values with Bonferroni adjustment.

Table S11. Results of Dunn's Kruskal-Wallis multiple comparisons identifying which education group differ significantly from each other, in relation to the proportion for bird (red) and mammal (blue) families poached. *p*-values with Bonferroni adjustment.

Table S12. Results of univariate regression analyses (OLS: Ordinary Least Squares) for the proportion of bird families each hunter socio-demographic group targeted in relation to regional conditions. Greater bird spectrum widths were significantly associated with greater regional wealth only for the hunter groups aged ≥ 41 and was significantly associated with lower educational attainment level for

all three hunter groups aged ≤ 50 . Spatial autocorrelation was tested using Moran's I, Lagrange multiplier and Robust Lagrange multiplier (in parentheses) diagnostic tests. When spatial dependence was identified, a spatial lag model (SLM) and/ or spatial error model (SEM) was used to re-estimate the model with maximum likelihood approach while controlling for spatial dependence. Bold highlighting indicates when the model effectively explained the proportion of prey families poached.

Table S13. Results of univariate regression analyses (OLS: Ordinary Least Squares) for the proportion of mammal families each hunter socio-demographic group targeted in relation to regional conditions. Greater mammal spectrum widths were also significantly associated with greater regional wealth for all three hunter groups aged ≥ 41 , as well with their educational attainment level; these same correlations were significant and negative for the two hunter groups aged 40 and under. Spatial autocorrelation was tested using Moran's I, Lagrange multiplier and Robust Lagrange multiplier (in parentheses) diagnostic tests. When spatial dependence was identified, a spatial lag model (SLM) and/or spatial error model (SEM) was used to re-estimate the model with maximum likelihood approach while controlling for spatial dependence. Bold highlighting indicates when the model effectively explained the proportion of prey families poached.

Table S14. Univariate phylogenetic generalised least squares regressions of bird family nestedness contributions on national and provincial network predictors. Body mass predicts bird nestedness contribution nationally. Protection status, protection status under China's List of Fauna under Special State Protection (1989); Ln(body size), Ln-transformed body mass; *N*, number of families; β , regression coefficient; λ , a measure of phylogenetic signal of traits or of trait relationships in PGLS models. Bold highlights indicate when the model effectively explained the nestedness contribution.

Table S15. Univariate phylogenetic generalised least squares regressions of mammal family nestedness contributions on national and provincial network predictors. Protection status predicts mammal nestedness contribution nationally. Protection status, protection status under China's List of Fauna under Special State Protection (1989); Ln(body size), Ln-transformed body mass; *N*, number of families; β , regression coefficient; λ , a measure of phylogenetic signal of traits or of trait relationships in PGLS models. Bold highlights indicate when the model effectively explained the nestedness contribution.

Table S16. Results of univariate regression analyses (OLS: Ordinary Least Squares) for nestedness contribution of twenty-six bird families involved in over 12 provincial networks in relation to regional conditions. The targeting intensities of the Accipitridae, Leporidae and Mustelidae were significantly greater in provinces with greater regional wealth. Spatial autocorrelation was tested using Moran's I, Lagrange multiplier and Robust Lagrange multiplier (in parentheses) diagnostic tests. When spatial dependence was identified, a spatial error model (SEM) was used to re-estimate the model with maximum likelihood approach while controlling for spatial dependence. Bold highlights indicate when the model effectively explained the nestedness contribution.

Table S17. Results of univariate regression analyses (OLS: Ordinary Least Squares) for nestedness contribution of mammal families involved in over 10 provincial networks in relation to regional conditions. The targeting intensity of the Felidae was significantly greater in provinces with lower per capita income. Spatial autocorrelation was tested using Moran's I, Lagrange multiplier and Robust Lagrange multiplier (in parentheses) diagnostic tests. When spatial dependence was identified, a spatial error model (SEM) was used to re-estimate the model with maximum likelihood approach while controlling for spatial dependence. Bold highlights indicate when the model effectively explained the nestedness contribution.

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